

SPECIFICITY AND EVOLUTION OF THE ANOPOLOCEPHALATE CESTODES OF MARSUPIALS

BY

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By far the most prominent group of cestodes occurring in marsupials are the anoplocephalates, being represented by 8 genera and numerous species. By contrast, there is only one known dilepid, 3 known hymenolepidid species, 3 davaineids and 2 taeniids. Furthermore, because the anoplocephalates occur in both the Australian and South American marsupials they provide an interesting subject for phylogenetic analysis. In the present analysis, the Anoplocephalata is considered to have two distinct families, the Linstowiidae and the Anoplocephalidae. Discussion of the latter family is limited to the sub-family Anoplocephalinae *sensu* Spasskii (1951).

1. — THE LINSTOWIIDS

The type genus *Linstowia* is one of the few parasite genera known to occur in both the South American and Australian marsupials. The type species, *L. echidnae*, occurs in the monotreme *Tachyglossus aculeatus* in Australia, but another species, *L. semoni*, occurs in bandicoots (*Perameles*, *Isodon*) of the family Peramelidae and in the native cats (*Dasyurus*) of the family Dasyuridae. In addition, a third undescribed species of *Linstowia* occurs in *Isodon*. In South America, *L. jheringi* and *L. bivittata* occur in a variety of opossums all belonging to the family Didelphidae.

A second linstowiid genus, *Oochoristica*, also occurs in both groups of marsupials, with 2 species in South American didelphoids, 2 species in Australian dasyurids and an undescribed species in Australian peramelids. However, unlike *Linstowia*, species of *Oochoristica* also occur in eutherian mammals and reptiles on several continents, complicating their phylogenetic analysis.

Anoploptaenia dasyuri, a parasite of the large dasyurids, *Sarcophilus* and *Dasyurus*, has generally been placed in the family Taeniidae. Indeed, Gregory *et al.* (1975) and Beveridge *et al.* (1975) have shown that the possession of a taeniid-like egg with an embryophore composed of blocks and the use of a mammalian intermediate host rather than an insect support this taxonomic position. However, the morphogenesis of the metacystode is typically that of a linstowiid (Beveridge *et al.*, 1975) and it may be argued that *A. dasyuri* is in fact a highly modified linstowiid having developed certain morphological and biological characters in parallel with the taeniids which are otherwise restricted to the Eutheria.

Apart from *Anoploptaenia*, true Linstowiids have insects as intermediate hosts and occur in hosts which are partly or wholly insectivorous. Hence in Australia they are restricted to the polyprotodont (carnivorous) marsupials.

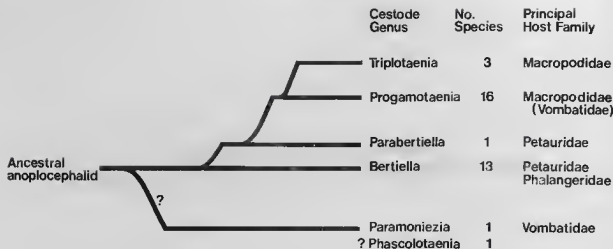


FIG. 4. — Dendrogram of possible phylogenetic relationships of anoplocephalid cestodes of Australasian marsupials.

2. — THE ANOPLOCEPHALIDS

Anoplocephalid cestodes occur in each of the major groups of herbivorous (diprotodont) marsupial in Australia but *not* in the South American marsupials. The genera *Bertiella* (9 described species) and *Parabertiella* (1 species) occur in large arboreal possums of the families Phalangeridae and Petauridae. Small members of the Petauridae and possums of the Burramyidae are not known to be parasitised by anoplocephalid cestodes. In addition, four species of *Bertiella* occur in *Phalanger* spp. in New Guinea and nearby islands. Other species of *Bertiella* have an unusual host distribution, occurring in rodents in Australia, Asia and Africa, dermopterans in the Phillipines and primates of the New and Old Worlds.

Two related marsupial families, the Phascolarctidae (koalas) and the Vombatidae (wombats), contain very different cestode parasites. Koalas are parasitised by *Bertiella obesa*, which may reflect the similar arboreal habits of both koalas and possums rather than indicate close phylogenetic affinities. Wombats are parasitised by two genera, *Phascolotaenia* and *Paramoniezia*, which have paired genitalia, unlike *Bertiella* and *Parabertiella*, but their affinities are not clear.

The principal cestode genus occurring in the Macropodidae is *Progamotaenia*, a genus with paired genitalia in which 16 species are described and there are 3 known undescribed species. Fourteen of the described species occur exclusively in macropodid hosts; one species occurs in vombatid hosts and one species occurs in both groups. Within the Macropodidae, no species of *Progamotaenia* are known from the subfamily Hypsiprymnodontinae, one species occurs in the rufous rat kangaroo *Aepyprymnus rufescens* belonging to the subfamily Potoroinae, and the remaining species occur in the large kangaroos and wallabies of the sub-family Macropodinae.

The genus *Triplotaenia* was considered for many years to be based on teratological specimens, but this is no longer the case and the genus now contains three valid species, all occurring in macropodids. In all species, two greatly twisted and fimbriated strobilae arise from a single scolex.

With certain exceptions therefore, each cestode genus belongs to a separate family or pair of closely related marsupial families. The exceptions are *Bertiella obesa* occurring in the koala, and the distribution of species of *Bertiella* occurring in the Phalangeridae and in only some species of Petauridae. The intermediate hosts of anoplocephalid cestodes are oribatid mites. The hosts are normally herbivores, and the mites are ingested incidentally on the food.

3. — RELATIONSHIPS WITHIN THE ANOPLOCEPHALID CESTODES

The cestode genera found in possums (*Bertiella*, *Parabertiella*) both have single genitalia and are considered to be ancestral to the genus *Progamotaenia* whose members have paired genitalia. The view that cestodes with paired genitalia arose (polyphyletically) from those with single genitalia is now generally accepted (Spasskii, 1951) and appears to have occurred in the marsupial anoplocephalids since singular morphological features such as the occurrence of vaginal atrophy following insemination, a conical pyriform apparatus with numerous reflected filaments, a narrow tube-like vagina enlarging suddenly into an almost spherical seminal receptacle and proglottis fringing all occur in some species of *Bertiella* or in *Parabertiella* but are major morphological features characterising the genus *Progamotaenia*. Similarly the testes which form a single band anterior to the uterus in most *Bertiella* species show a slight tendency to divide into two groups in *B. pseudochiri* and *B. petaurina*, whereas species of *Progamotaenia* may have testes arranged in a single group or in two separate groups, predominantly the latter. It is believed therefore that the genus *Progamotaenia* arose from *Bertiella* or *Parabertiella* — like ancestors by a doubling of the genitalia and that similarities between *Progamotaenia* and the double — pored cestodes of eutherian mammals notably *Ctenotaenia* and *Mosogovoyia*, are due to convergence. Species of *Progamotaenia* with the genitalia completely separated in the two halves of the proglottis are considered derived forms which, by longitudinal division of the entire strobila have given rise to the genus *Triplotaenia*, formerly considered to be a teratological deformity but now known to be a valid genus with three species.

Accepting this general pattern of relationships, one can infer that the paired uteri in *Progamotaenia* is a derived state and that the single uterus is an ancestral state. Also, the proglottis fringing, developed to such a high degree in species such as *P. villosa*, is a derived and not ancestral character. These two features can be used to conveniently divide up the genus *Progamotaenia* along with the degree of development of the cirrus sac (which may be very powerfully developed with a coiled, heavily armed cirrus or may be weakly developed and unarmed) and the occurrence of the parasite in the intestine or in the hile duct of the host. Using such characters, an arrangement of the species (as shown in Table 1) is arrived at.

4. — CORRELATION WITH HOST TAXONOMY

As mentioned above, Australian species of *Bertiella* have an unusual host distribution, occurring in the Phalangeridae, in some species of Petauridae and in the distantly related Phascolarctidae. Rather than indicating host taxonomic relationships, the distribution most probably reflects feeding behaviour. Members of the Phalangeridae and Phascolarctidae are arboreal herbivores, as are those members of the Petauridae which are parasitised by *Bertiella* spp. By contrast, petaurids which do not have cestode parasites, as well as the Burramyidae are nectar and insect feeders. Cestode species that do occur in phalangerids are distinct from those which occur in petaurids.

Within the genus *Progamotaenia*, the "fringed" species (*P. zschokkei*, *P. villosa*, *P. lagorchestis*, *P. spearei*, *P. thylogale*, *P. proterogyna*) form a distinctive group within the genus, and, with the exception of *P. proterogyna* and *P. zschokkei*, are restricted to the macropodid genera *Thylogale* and *Lagorchestes*. The three undescribed species also fit into this group and occur in *Thylogale* in Australia and *Dorcopsis* in New Guinea. With the exception of *P. thylogale* which occurs throughout the range of the host genus (*Thylogale*), this group of cestode species (including *P. proterogyna*) is limited to hosts in northern Australia and New Guinea. Most species are host specific, and *P. zschokkei* seems a likely ancestor for the whole group.

Amongst the "unfringed" species, a group of 3 species (*P. bancrofti*, *P. aepyprymni*, *P. johnsoni*) stands out on the basis of the enormous development of the cirrus and cirrus sac. They are host specific and occur in the macropodine genera *Lagorchestes* and *Onychogalea* and in the potoroine genus *Aepyprymnus*. All occur in northern Australia only. The remaining species of *Progamotaenia*

are un-fringed and have a weakly developed cirrus sac. With one exception (*P. festiva* which is considered in detail below) they are restricted to the large kangaroos and wallabies of the genera *Wallabia* and *Macropus*. Two species are known from single hosts while the others occur in a number of host species. *P. ewersi* occurs in northern and southern Australia, whereas *P. macropodis*, *P. ruficola* and *P. effigia* are essentially southern species.

Two cestode groups occur almost exclusively in small, older wallabies of the genera *Lagorchestes*, *Thylgale*, *Onychogalea* and *Petrogale* and the higher degree of host specificity of species in this group may reflect a longer association between host and parasite. The third cestode group of 4 species (*P. festiva* excepted) occur in the very recent genus *Macropus* and the associated genus *Wallabia*, and the lower degree of specificity may reflect their more recent origins and hence the much closer relationships between the hosts. The division of the Macropodinae into the two major groups indicated is not currently recognised in the taxonomy of the hosts, though recent serological evidence presented by Kirsch (1977) indicates just such a division as is indicated by the cestode parasites. Kirsch's data supports morphological data in placing *Wallabia* very close to *Macropus*, and this association is supported by data derived from the cestodes.

Of the 15 species of *Progamotaenia* in macropodids, 14 occur in macropodines and only one in potoroinae. This data may be taken as general support for the current taxonomic distinction made between the host subfamilies, although the single species *P. aepyprymni* in *Aepyprymnus rufescens* would suggest a relationship between this host and the genera *Onychogalea* and *Lagorchestes*.

The hypothesis that *Progamotaenia* and *Triplotaenia* are derived from *Bertiella*-like ancestors accords well with the view that the macropodids are derived from possum like ancestors. The distinctiveness of the wombat cestodes parallels the fact that the wombats diverged much earlier in the evolutionary history of the marsupials, but the precise relationships of the cestodes remains an enigma. They may have arisen from *Bertiella*-like ancestors by duplication of the genitalia in a separate development to that producing *Progamotaenia*, but the hypothesis is not easy to sustain. The genera *Progamotaenia* and *Triplotaenia* are considered the most recent, and they occur in the most recently evolved hosts, indicating a good correlation with host evolution.

5. — SPECIFICITY

The foregoing analysis is based primarily on cestode species which show a relatively high degree of host specificity and indicates that if hosts were allocated to taxonomic groups on the basis of their cestode parasites, the host arrangement would closely resemble current taxonomy at the supra-generic level. Little or no information is provided on relationships within host genera. *Progamotaenia festiva*, which occurs in 10 host species would, at first sight offer little phylogenetic information. However, it is a polymorphic species, as currently defined in morphological terms, and may consist of a complex of highly specific sibling species which may provide very valuable information about host phylogeny. This possibility is shown by the apparently anomalous situation which exists with the bile duct inhabiting species *P. festiva* and *P. effigia*, the former occurring in 6 genera of macropodids, the latter occurring only in *Macropus fuliginosus*. *P. festiva* was first described in *Macropus giganteus*, a host very similar to *M. fuliginosus*, the 2 hosts having been confused by many workers until as recently as 1972 (see Kirsch and Poole, 1972). The two cestodes are apparently host specific and where two macropodid species (one parasitised by *P. festiva* and the other by *P. effigia*) graze together, no cross transmission occurs (Beveridge, 1976, Arundel *et al.*, 1980). The two cestode species differ only in the number of uteri per proglottis, but the character does not vary within either species. However, preliminary results using electrophoretic techniques suggest that the taxonomic conclusions based on morphology may need qualification. Limited data so far obtained by P. Baverstock and M. Adams (unpublished) suggest that *P. effigia* from *M. fuliginosus* and *P. festiva* from *M. giganteus* are very similar genetically, differing at only one locus. By contrast, specimens of "*P. festiva*" from different host species are genetically quite different, suggesting the existence of a complex of sibling species. The genetic data in contrast to morphology, indicates a relationship between the cestodes more akin

to the relationships known to exist between the hosts, and suggest that care is needed in interpreting situations where information on host and parasite taxonomy disagree.

6. — EVOLUTION OF THE CESTODES OF MARSUPIALS

The genus *Linstowia* provides a very obvious connecting link between the South American and Australian marsupials. In the latter group, it occurs only in the Dasyuridae and Peramelidae (the Carnivorous polyprotodonts), and these two groups are most closely related to the South American carnivorous didelphoids (Kirsch, 1976) whose ancestors are thought to have invaded Australia via Antarctica. In Australia, the linstowiids seem to have radiated very little in spite of major radiations in both the Dasyuridae and Peramelidae. A major exception may be *Anoplostaenia* which has made the transition from an insect to a mammal as intermediate host and hence parasitises the larger marsupial carnivores, having at the same time evolved convergently with the taeniids of eutheria.

The linstowiids do not seem to have adapted to the evolution of the very large groups of herbivorous marsupials presumably because insect intermediate hosts were now unsuitable for parasite transmission and the explosive radiation of the Phalangerioidea therefore resulted in large numbers of mammal species without any intestinal cestode parasites. These unoccupied niches were subsequently filled by the anoplocephalids which having oribatid mites as hosts could readily infect the grazing or browsing herbivores which had evolved. They did not however infect the nectar-feeding possums and hence no cestodes are known from the Burramyidae and certain Petauridae.

The origins of the true anoplocephalids can be clearly traced to the genus *Bertiella*, and this same genus has an unusual host distribution, occurring in Australian marsupials, rodents, dermopterans and primates. Since we know that the rodents invaded Australia from islands to the north of the continent, the most simple hypothesis is that the genus *Bertiella* was brought to Australia by the rodents and because of the use of oribatids as intermediate hosts was able to spread to the herbivorous marsupials, occupying the large number of vacant niches. On the basis of published records, *Bertiella anapolytica* is known only from *Rattus* species in Australia and Malaysia, and *Rattus* species invaded Australia only 1 million years ago, a time span which would hardly allow for the extensive radiation of the Australian anoplocephalids. However, the writer has also collected this species from another rodent, *Uromys caudimaculatus*, which came to Australia in the Miocene, 15-20 millions years ago (Watts and Aslin, 1980). If a host such as *Uromys* was the host of *B. anapolytica* in the Miocene, we have a simple explanation for the entry of the anoplocephalids to Australia from the north, their absence in South American marsupials and for the explosive radiation of the anoplocephalids which occurred as they filled a variety of unoccupied niches left unoccupied by the original linstowiid parasites of the dasyurids and peramelids.

TABLE 1. — Species of Linstowiid cestodes from Australian* and South American† marsupials.

Cestode	Host Genus	No. host species
<i>Linstowia semoni</i> *	<i>Isodon, Dasyurus</i>	2
<i>L. sp. undescribed</i> *	<i>Isodon</i>	1
<i>L. jheringi</i> †	<i>Didelphys, Marmosa, Metachirus, Metachirops, Peromys</i>	5
<i>L. bivittata</i> †	<i>Didelphys, Marmosa, Metachirus, Caluromys</i>	9
<i>Anoplostaenia dasyuri</i> *	<i>Sarcophilus, Dasyurus</i>	3
<i>Oochoristica antechini</i> *	<i>Antechinus</i>	1
<i>O. eremophila</i> *	<i>Antechinus</i>	1
<i>O. didelphidis</i> †	<i>Marmosa</i>	2
<i>O. marmosae</i> †	<i>Marmosa</i>	1
<i>O. surinamensis</i> †	<i>Didelphys</i>	2

TABLE 2. — Species of Anoplocephalid cestodes from Australasiad marsupials with hosts and number of host species.

Cestode	Host genus	No. Host Species
<i>Progamotaenia villosa</i>	<i>Lagorches</i>	1
<i>P. lagorches</i>	<i>Lagorches</i>	1
<i>P. spearei</i>	<i>Thylogale</i>	1
<i>P. thylogale</i>	<i>Thylogale</i>	3
<i>P. proterogyna</i>	<i>Macropus agilis</i>	1
<i>P. zschokkei</i>	<i>Thylogale, Petrogale, Onychogalea, Macropus agilis, Lagorches</i>	6
<i>P. bancrofti</i>	<i>Onychogalea</i>	2
<i>P. johnsoni</i>	<i>Lagorches</i>	1
<i>P. acyprymni</i>	<i>Aepyprymnus</i>	1
<i>P. ewersi</i>	<i>Macropus, Wallabia</i>	8
<i>P. macropodis</i>	<i>Macropus, Wallabia</i>	5
<i>P. ruficola</i>	<i>Macropus rufus</i>	1
<i>P. festiva</i>	<i>Macropus, Wallabia, Petrogale, Onychogalea, Setonix, Lagorches</i>	10
<i>P. effigia</i>	<i>Macropus fuliginosus</i>	1
<i>Triplotaenia mirabilis</i>	<i>Petrogale</i>	1
<i>T. undosa</i>	<i>Macropus, Wallabia</i>	4
<i>T. fimbriata</i>	<i>Macropus, Petrogale</i>	3
<i>Phascolataenia comani</i>	<i>Vombatus</i>	1
<i>Paramonixia johnstoni</i>	<i>Vombatus, Lasiiorhinus</i>	2
<i>Parabertiella campanulata</i>	<i>Pseudocheirus</i>	2
<i>Bertiella aberrata</i>	<i>Pseudocheirus</i>	2
<i>B. pseudochiri</i>	<i>Pseudocheirus</i>	1
<i>B. undulata</i>	<i>Pseudocheirus</i>	1
<i>B. pellucida</i>	<i>Pseudocheirus</i>	1
<i>B. foederata</i>	<i>Pseudocheirus</i>	1
<i>B. petaurina</i>	<i>Schoinobates</i>	1
<i>B. mawsonae</i>	<i>Schoinobates</i>	1
<i>B. trichosuri</i>	<i>Trichosurus</i>	2
<i>B. rigida</i>	<i>Phalanger</i>	1
<i>B. sarasinorum</i>	<i>Phalanger</i>	1
<i>B. kapul</i>	<i>Phalanger</i>	1
<i>B. edulis</i>	<i>Phalanger</i>	1
<i>B. obesa</i>	<i>Phascolarctos</i>	1

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DISCUSSION

- BURT. — Are oribatid mites the hosts of Australian anoplocephalids ?
- BEVERIDGE. — We do not know for certain. Dr. D. Spratt has studied the problem for several years and development of some species certainly occurs in oribatids, but no cycles were completed.
- BURT. — Any naturally infected mites ?
- BEVERIDGE. — Yes, but since the scoleces are unarmed, they cannot be identified with any certainty.
- FAIN. — Does *Bertiella* occurs in primates also ?
- BEVERIDGE. — Yes, but the genus *Bertiella* is at present a taxonomic mess and it is really impossible to be dogmatic about the species.
- CZAPLIŃSKI. — Are the Hymenolepididae closely related to the Anoplocephalidae ? Do you think that vaginal atrophy occurring in Hymenolepidids and Anoplocephalids indicates a close relationship between the two groups ?
- BURT. — Evidence from their larval structure suggests that they are closely related as they both have a true, "double" cysticeroid, the cercoecystis type of cysticeroid of Villot and not the "single" monocercus type or cercoscolex type found in the Dilepididae.
- EUZET. — Vous estimez que les Anoplocephalidae sont arrivés en Australie avec les Rongeurs et qu'ils se sont diversifiés chez les Marsupiaux herbivores. Pour quelles raisons les Hymenolepididae, qui sont aussi nombreux chez les Rongeurs, n'ont-ils pas réussi ce passage ?
A-t-on une idée de l'importance relative Anoplocephalidae-Hymenolepididae chez les Rongeurs du Sud-Est Asiatique ?
Est-ce que l'on pourrait lier cette absence d'Hymenolepididae à la taille des hôtes ?
- VAUCHER. — Les *Hymenolepis*, de même que les *Taenias* et les *Davainaeidae*, n'ont pas très bien réussi en Australie et l'on peut se demander s'ils ne sont pas arrivés après les Anoplocephalidae et se sont ainsi trouvés en compétition avec une forme déjà installés.
- CROMPTON. — What are precisely the biochemical differences that you are looking at in cestodes ?
- BEVERIDGE. — Different enzymes ; and whether they are present or absent in each species.
- CROMPTON. — If you find biochemical differences does it mean that there are really different species ?
- BEVERIDGE. — We must face this problem when we come to it, by combining any biochemical data with morphology. Results to date are merely preliminary as we have only screened 10 enzymes in a few species. We hope to screen 40 enzymes in a variety of specimens from different hosts.
- HOFSTETTER. — Il est remarquable de constater l'accord parfait de l'histoire des Cestodes australiens (*Linstowia* et *Bertiella*) avec les idées modernes sur le peuplement mammalien de l'Australie : arrivée ancienne des Marsupiaux didelphoïdes via Antarctide depuis l'Amérique du Sud ; migration tardive des Rongeurs est-asiatique après déplacement de l'Australie vers le Nord. L'étude et l'interprétation offertes par le Dr. Beveridge ont à cet égard une valeur exemplaire.